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Population Characteristics of Coyotes (Canis latrans) in the Northern Chihuahuan Desert of New Mexico

LAMAR A. WINDBERG,[1] STEVEN M. EBBERT[2] AND BRIAN T. KELLY[3]

U.S. Department of Agriculture, Animal and Plant Health Inspection Service,
Denver Wildlife Research Center, Utah State University, Logan 84322-5295

ABSTRACT.—We estimated demographic variables for a coyote (*Canis latrans*) population in the northern Chihuahuan Desert in spring 1991. Indices of coyote abundance indicated that the population was in a decline phase during 1991. Of 41 coyotes radio-collared on the Jornada Experimental Range near Las Cruces, New Mexico, only 7% were juveniles and a relatively high percentage (40%) were transient (nonterritorial) animals. Size of the core areas of 10 territorial ranges occupied by 13 coyotes averaged 5.6 km². None of 11 radio-collared females produced viable fetuses in 1991. We examined data from earlier studies to assess factors affecting population dynamics in the region. Autumn scent-station indices of coyote abundance were positively correlated with annual rainfall (July to June) during 1972–1981. Low recruitment in the population during 1991 may have resulted from the combined effect of relatively low rainfall and high coyote abundance in the preceding 2–3 yr.

INTRODUCTION

Coyote (*Canis latrans*) population dynamics are influenced by interactions between their social organization and food availability (Knowlton and Stoddart, 1983; Windberg, 1995) and by the degree of human exploitation (Knowlton, 1972; Davison, 1980). Demography (Todd and Keith, 1983; Gese *et al.*, 1989; Windberg, 1995) and social structure (Camenzind, 1978; Andelt, 1985) vary locally within the coyote's diverse geographic range.

The Chihuahuan Desert (355,000 km²) encompasses most of N-central Mexico and extends northward into southern New Mexico and western Texas (Schmidt, 1979). Temporal fluctuations in density and diversity of rodent populations in the Chihuahuan Desert are related to variations in forage (Whitford, 1976; Hallett, 1982; Brown and Heske, 1990), which are influenced by annual rainfall. Although rainfall and prey abundance potentially affect dynamics of coyote populations, demographic analyses for coyotes in this region are limited.

We collected population data for coyotes in conjunction with a study of predation on livestock (Windberg *et al.*, 1997). Our objectives were to estimate age and sex distributions, natality, and social composition of the population during spring 1991, examine long-term coyote population trends in the region, and investigate factors influencing dynamics of this population.

METHODS

The 75 km² study area was located on the northern portion of the U.S. Department of Agriculture (U.S. Dep. Agric.) Jornada Experimental Range (JER), 40 km N of Las Cruces, Dona Ana County, New Mexico. The 783-km² JER is characterized by basin topography representative of the northern Chihuahuan Desert (Hennessy *et al.*, 1983). The elevation

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[1] Corresponding author: P.O. Box 921, Blackfoot, Idaho 83221

[2] Present address: U.S. Fish and Wildlife Service, P.O. Box 1938, Homer, Alaska 99603

[3] Present address: Hill's Pet Nutrition, Inc., Science and Technology Center, P.O. Box 1658, Topeka, Kansas 66601-1658

of the study area ranged from 1320 to 1390 m. The climate is arid, with annual precipitation concentrated in late summer (Hennessy *et al.,* 1983). Invading mesquite (*Prosopis glandulosa*) occurs on most of the plains, and large dunefields have formed on the predominantly sandy soils (Buffington and Herbel, 1965). Permanent water on the study area was limited to one earthen impoundment and three livestock water troughs during spring 1991. The primary prey of coyotes on the JER during the study appeared to be lagomorphs and rodents based on our cursory examination of coyote feces on the area.

We trapped (3431 trap days) and radio-collared coyotes from 19 February to 21 March 1991 (plus one coyote in November 1990). We used foothold traps with tranquilizer tabs containing 600 mg of propiopromazine hydrochloride to reduce injury and trauma to captured coyotes (Balser, 1965). We measured body mass and length (tip of nose to base of tail) of each coyote, and extracted a vestigial premolar tooth for age analysis. We recovered radio-collared coyotes by aerial shooting during 29–31 May 1991. We removed canine teeth from all coyotes recovered, and preserved and examined ovaries and uteri of females as described by Windberg (1995). Microscopic sections of canine, or premolar teeth, were prepared by Matson's Laboratory (Milltown, Mont.) for estimation of coyote age based on patterns of cementum layers (Linhart and Knowlton, 1967). We report coyote age to the nearest year, which approximated their age during the radio-tracking period.

We determined locations of radio-collared coyotes by fixed-station triangulation from 30 March to 29 May 1991. The radio-telemetry receiving stations were two portable shelters paired at various combinations of 11 locations. Radio-telemetry receivers were connected to arrays of two 5-element yagi antennas stacked horizontally on a 6-m tower and coupled out-of-phase (null system) with a hybrid junction. We maintained antenna orientation with a reference radio-transmitter positioned at known azimuths from the receiving stations. We determined positions of receiving stations and the reference transmitter with Global Positioning System (GPS) (Trimble Navigation Ltd., Sunnyvale, Calif.) technology. We determined coyote locations at 20–60 min intervals from 1 h before sunset until 1 h after sunrise. Because topographic relief was inadequate for complete radio-telemetry coverage of the study area, we collected data systematically from segments of the area by alternating various pairs of receiving stations at intervals of 1–5 days. We also collected standardized data to estimate the frequency of occurrence of coyotes within radio-telemetry range of receiving stations by systematic scans for signals from all radio transmitters two to four times per night (Table 1). To assess the precision of the radio-telemetry system, we covertly placed two test radio transmitters at 10 known locations (Mills and Knowlton, 1989), as determined by GPS, over 10 nights of routine monitoring.

We converted point-estimates of coyote locations derived from paired azimuths to Universal Transverse Mercator coordinates. Paired azimuths with differences of <20° or >160° were discarded to eliminate locations derived from extremely acute and obtuse angles of intersection. We analyzed point-estimate data with program HOME RANGE (Ackerman *et al.,* 1990), using a 48 × 21 grid with a scale of 1000 m per grid (except for 2000 m per grid for five coyotes with larger ranges). We excluded outlier locations identified by the program in the initial analysis from the final estimates of range shape and size. We delineated boundaries of coyote ranges for the 75% and 85% harmonic-mean estimates of their activity areas, and also computed the core areas of ranges (Ackerman *et al.,* 1990). We classified marked coyotes as territorial or transient (nonterritorial) based on the areal distribution of radio telemetry locations as described by Windberg and Knowlton (1988). Specifically, territorial coyotes occupied ranges with core areas exclusive of adjacent territorial individuals. We used the standardized data for frequency of occurrence of marked coyotes

TABLE 1.—Mean radio-telemetry sampling data and range sizes for social classes of coyotes on the Jornada Experimental Range, 30 March–29 May 1991

Variable	Territorial (n = 13)		Transient (n = 12)		Undetermined (n = 4)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Sampling data						
No. nights of radio-tracking	23	2	18	3	18	1
No. radio-telemetry point-estimates	99	18	66	14	51	5
Percent frequency during scans[a]	71	3	51	6	52	4
Range size (km²)						
Core area	5.6	0.6	16.2	4.0[b]	4.9	1.5
75% harmonic-mean estimate	9.1	1.2	19.9	5.1	7.8	2.3
85% harmonic-mean estimate	12.6	1.8	25.9	6.5	10.0	3.1

[a] Frequency of radio-tracking reception from two nearest receiving-stations during systematic scans for signals

[b] n = 9; no core areas delineated for three transients

at the two receiving stations nearest their range (Table 1) to aid in territorial classification, and to estimate social composition of the population.

We used two sets of data as indices of relative abundance of coyotes in the region. Four coyote scent-station surveys (Linhart and Knowlton, 1975) were conducted in Dona Ana and Sierra counties during 1972–1981 (U.S. Dep. Inter., 1972–1981). Each survey route consisted of 50 scent stations operated for 5 consecutive days in autumn (September) resulting in 1000 station-days/yr. The scent-station index of coyote abundance was reported as the proportion of stations visited multiplied by 1000 (U.S. Dep. Inter., 1972–1981). Additional coyote scent-station surveys using similar methods were conducted on the JER in September 1983 (500 station days) (Kumm, 1985) and October 1989 (250 station days) (Del Frate, 1990). We also derived indices of relative coyote abundance during 1987–1994 from records of the number of coyotes captured to reduce livestock depredations by field specialists of the U.S. Dep. Agric. Animal Damage Control Program in Dona Ana and Sierra counties. The same two specialists captured coyotes in those counties during all 8 yr, and used generally similar methods (traps, M44s, snares). The annual capture index of coyote abundance was the number of coyotes taken from 1 September of each year to 31 May of the following year per 100 h of work by the specialists. We multiplied the capture indices by 2.25 to adjust the numerical units to correspond with the scent-station indices (Fig. 1). The number of coyotes captured ranged from 199 to 588 and the number of hours worked ranged from 888 to 1318/yr. Both indices were based on similar behavioral responses by coyotes, although the sensitivity may have differed between the methods.

We used correlation analyses to examine the relationship between annual indices of coyote abundance and rainfall measured at 21 locations on the JER (NOAA, 1971–1994). Whitford (1976) and Brown *et al.* (1979) considered precipitation to be the ultimate factor affecting the dynamics of rodent populations by its effect on vegetation, seed and insect production. We summed annual rainfall for the biological year from July through June to account for the lag in primary production and prey population response (Whitford, 1976; Brown and Heske, 1990). We analyzed sex and age distributions among territorial classes with 2-tailed Fisher exact tests. We compared mean range sizes between sexes by t-test.
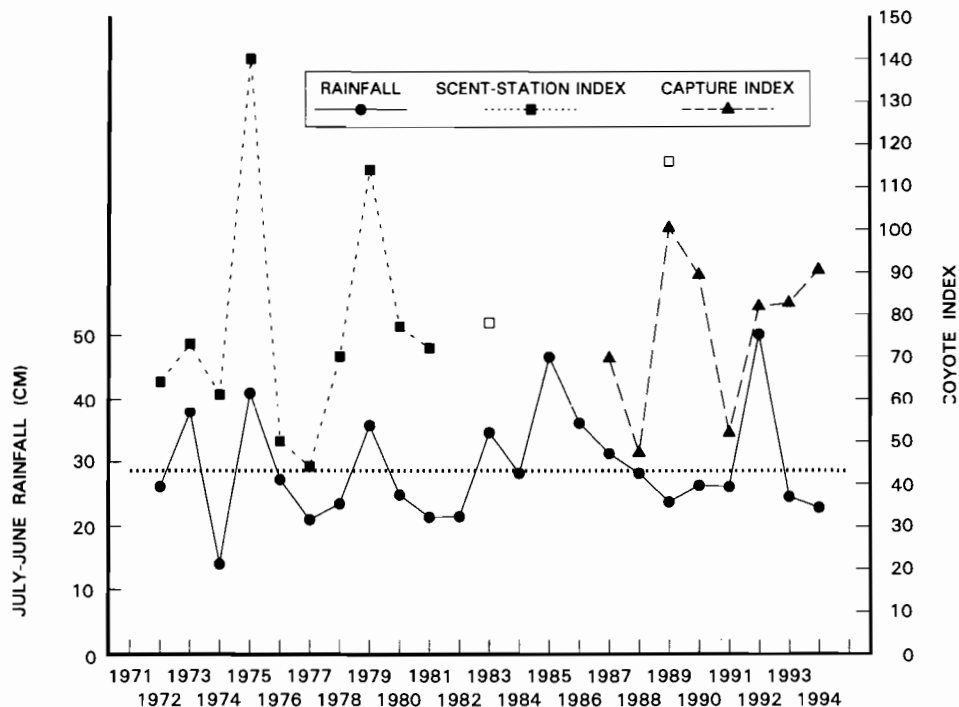
FIG. 1.—Scent-station and capture indices of coyote abundance in autumn-winter for Dona Ana and Sierra counties, New Mexico, and rainfall (cm) from June of prior year to July, 1971–1994. Scent-station indices for 1983 and 1989 (open squares) are from Krum (1985) and Del Frate (1990) (see Methods). Dotted line is mean annual rainfall (28.7 cm)

RESULTS

The indices of coyote abundance in Dona Ana-Sierra counties fluctuated during 1972–1994 with scent-station indices (CV = 38%) slightly more variable than capture indices (CV = 25%) (Fig. 1). Both scent-station and capture indices of abundance were available in 1989 and appeared to correspond well (116 vs. 100). Coyote abundance declined during the year (1990–1991) of our study (Fig. 1).

Annual rainfall fluctuated markedly above and below the long-term mean (28.7 cm) during 1972–1981 (Fig. 1) and the scent-station indices of coyote abundance were positively correlated with rainfall (r = 0.73, t = 2.8, df = 8, P = 0.02). The capture indices of abundance were not correlated with rainfall (r = 0.07, t = 0.2, df = 6, P = 0.99), but the associated rainfall pattern included 3 consecutive yr of above-average (1985–1987) and be-low-average (1989–1991) rainfall (Fig. 1).

Forty-one of 43 coyotes captured on the study area were radio-collared. The sample of 26 males and 17 females did not differ significantly from an even sex ratio (X^2 = 0.9, df = 1, P = 0.39). There were low percentages of younger coyotes as only 7% were juveniles (1 yr) and 12% were 2-yr old, whereas 72% were 3–7 yr and 9% were 8–12 yr. Mean masses of adult (≥3 yrs) males (n = 21) and females (n = 13) in February–March 1991 were 11.6 kg (SE = 1.4) and 9.5 kg (SE = 1.0), respectively. Mean body lengths were 88.0 cm (SE = 4.4) for males and 83.1 cm (SE = 3.0) for females.

Our radio-telemetry system had a mean error of 327 m (SE = 33) between point-estimates and known locations of test radio transmitters (n = 110). Large error distances were associated with a few (<10%) acute or obtuse angles of intersection for point-estimates >3 km from receiving stations. Most of such point-estimates would typically have been identified as outliers by program HOME RANGE and, hence, excluded from the analysis of coyote ranges according to our methodology. In spite of the error, we believe our data were acceptable for classification of the territorial status of coyotes and delineation of the relative location and size of their ranges, given the scale of the ranges.

A total of 2457 point-estimates for 29 radio-collared coyotes were accumulated during March–May 1991 (Table 1). An additional 572 estimates that were excluded from analyses due to poor angles of intersection provided supplemental information for territorial classification of some individuals. Gese *et al.* (1990) reported that a minimum of 28–36 point-estimates per individual over 5–9 nights, using sequential (nonindependent) locations taken at hourly intervals, were required to adequately delineate range size for resident coyotes. Using a similar sampling strategy, we estimated range size and territorial classification for 22 coyotes with 34–262 point-estimates per animal over 14–39 nights. We classified three additional coyotes with fewer point-estimates (7–16) as transients (nonterritorial) because the distribution of their locations indicated they had relatively large, and therefore nonexclusive, ranges. These individuals were frequently located (22–43% of systematic scans) on the study area, but, unfortunately, the point-estimates for them were limited because they were usually beyond the range of one of the paired receiving stations. Four coyotes with 41–64 point-estimates had relatively small ranges when on the study area (Table 1), but we were unable to classify their status because they were present less frequently (t = 3.0, df = 15, P < 0.01) than territorial animals and were absent for several consecutive days. Twelve other marked coyotes were located too infrequently (0–19% of scans) to attempt classification.

Thirteen radio-collared coyotes were classed as territorial and 12 as transients (Table 1). The transients included six coyotes with large ranges which were located near receiving stations as frequently as territorial individuals [x̄ = 67% (SE = 7) vs. 71% (SE = 3) of scans]. The other six transients had relatively small disjunct areas of activity and were located near receiving stations less frequently [x̄ = 36% (SE = 4) of scans]. Based on an adjustment for the relative frequency of presence of the 13 territorial (x̄ = 71% of scans) and 12 transient (x̄ = 51% of scans) individuals on the study area (Windberg and Knowlton, 1988; Stoddart *et al.*, 1989), we estimated the social composition of the population included 60% territorial and 40% transient coyotes.

The percentage of young (1 and 2 yr) coyotes was similar among territorial (23%) and transient (25%) coyotes and no difference (X^2 = 2.1, df = 3, P = 0.73) in the overall age distribution was detected between territorial classes. Nor was there a difference (X^2 = 5.9, df = 6, P = 0.42) in the age distribution of unclassified coyotes compared with territorial and transient animals.

Because their core areas were generally exclusive, the spatial distribution of the 13 territorial coyotes indicated they occupied 10 territorial ranges (Fig. 2). Core areas of three territorial males and females overlapped (Fig. 2), suggesting they were members of the same social groups. Based on the relative size and location of core areas, we apparently failed to capture any member of several additional social groups that occupied intervening space on the study area. The limited water sources on the study area were located along edges of core areas (Fig. 2).

Mean size of the core areas of 13 territorial coyotes was 5.6 km² (SE = 0.6), and there were no detectable differences (t = 0.5, df = 11, P > 0.50) between territorial males (x̄ =
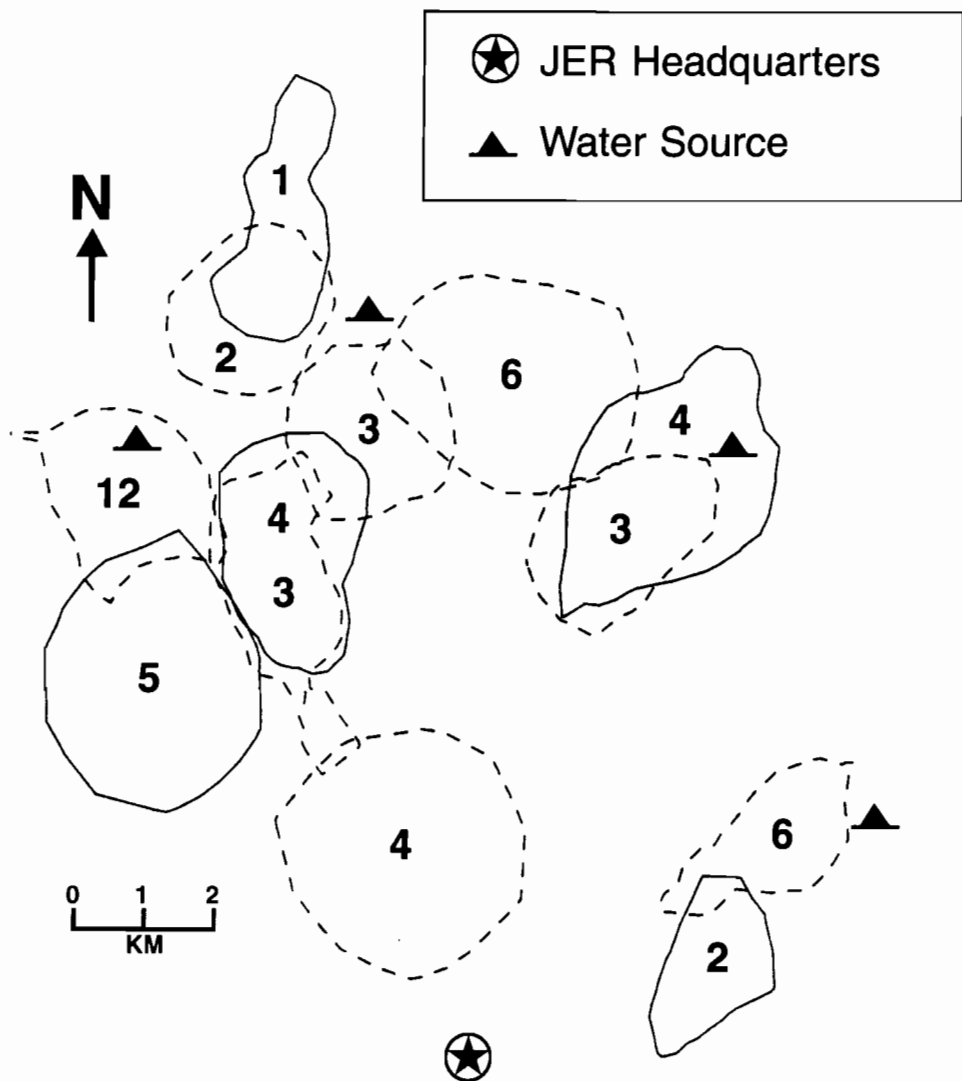
FIG. 2.—Spatial distribution of core areas of five male (solid lines) and eight female (dashed lines) territorial coyotes on Jornada Experimental Range, New Mexico, March–May 1991. Age (yr) of coyote is shown in each core area

5.9 km^2, SE = 0.7) and females ($\bar{x}$ = 5.4 km^2, SE = 0.5). Mean sizes of the ranges of territorial coyotes were 9.1 km^2 (SE = 1.2) and 12.6 km^2 (SE = 1.8) for the 75% and 85% harmonic-mean estimates, respectively (Table 1). Mean ranges for the six transients that occupied the study area as frequently as territorial residents were 35.3 km^2 (SE = 4.8) and 45.4 km^2 (SE = 5.7) for the 75% and 85% estimates.

The low proportion of young coyotes captured on the study area indicated that the population had low recruitment during the 2 preceding yr. Based on examination of uteri and

ovaries of radio-collared coyotes, none of 11 females (seven territorial, four transient) had viable fetuses during 1991. Only one of four territorial females (2–12 yr of age) that ovulated had implanted, but it resorbed all fetuses. The three territorial females that failed to ovulate were 3, 4 and 6 yr old.

DISCUSSION

Human exploitation of coyotes for sport-hunting and livestock protection reportedly occurs on much of the public and private land surrounding the JER (Howard and Del Frate, 1991). Howard and Del Frate (1991) reported that ≥53 coyotes were removed from a part of the JER (783 km^2) directly S of our study area in 1988, and ≥50 in 1989, to reduce depredations on livestock. In 1983–1984, 28 coyotes were removed from the JER for research (Kumm, 1985).

Rainfall patterns are a useful index of prey abundance because long-term studies of rodents in the Chihuahuan Desert showed densities were correlated with forage availability, indicating that populations responded to variation in precipitation, primary production and availability of food resources (Whitford, 1976; Hallett, 1982; Brown and Heske, 1990). Davis et al. (1975) reported short-term fluctuations in lagomorph abundance associated with variation in rainfall in southeastern New Mexico. The abundance of lagomorphs and rodents tended to fluctuate together in other southern arid regions (Henke, 1992; White and Ralls, 1993; Windberg, 1995). Rogers (1965) found lagomorphs (49% volume) and rodents (25% volume) predominant in stomachs of coyotes collected near our study area. Lagomorphs and rodents were also staple prey for coyotes in other southwestern localities (Ortega, 1987; Windberg and Mitchell, 1990; Henke, 1992). A trend for the coyote population we studied in the northern Chihuahuan Desert to fluctuate annually with rainfall, based on 10 yr of scent-station indices of abundance during 1972–1981, suggests a numerical response to varying abundance of prey. However, the capture indices of coyote abundance in our study did not exhibit a similar relationship with annual rainfall. The inconsistency may have been attributable to much less variability in rainfall during 1987–1994 in contrast with the relatively sharp fluctuations during 1972–1981, or unidentified factors which may have offset the effects of rainfall.

During our study, the coyote population was in decline from relatively high abundance in autumn 1989 to low abundance in autumn 1991. Low recruitment before and during spring 1991 was the immediate mechanism of population decline. The percentage of juveniles (7%) in our population sample on JER was extremely low in spring 1991, and our small sample of females indicated extremely low natality for that year. Recruitment in coyote populations elsewhere in the northern Chihuahuan Desert ranged from 23 to 53% juveniles in five other studies (Table 2).

Previous studies suggest natality is typically low among coyotes in the Chihuahuan Desert. Linhart et al. (1968) reported 54% of 43 females (adults and juveniles combined) had fetuses or placental scars at Fort Bliss, New Mexico, in 1965 and 36% (n = 28) at Deming, New Mexico, in 1966. Fowler (1979) reported 48% of 58 adults and 7% of 30 juveniles ovulated in Grant-Hidalgo counties, New Mexico, in 1978. Littauer (1980) found 63% of adult females (n = 68), but no juveniles (n = 15), ovulated on the same site in 1979. Rogers (1965) had a mean of 4.3 placental scars among 11 females in Dona Ana County, New Mexico, during 1964–1965. The absence of reproduction among coyotes in our sample from spring 1991 was unprecedented. Windberg (1995) found natality limited to territorial adult females in a high-density population. However, none of seven territorial adult females produced viable fetuses on the JER in 1991. It was especially unusual that three mature (3–6 yr) territorial females failed to even ovulate. Fowler (1979) reported that two of eight

TABLE 2.—Percent juveniles in coyote population samples for various localities in the northern Chihuahuan Desert of New Mexico

Year	Locality	n	Percent juveniles	Reference
1964–1965	Dona Ana County	137	53	Rogers, 1965
1966	Luna County	73	32	Linhart and Brusman, 1966
1978	Grant-Hidalgo County	185[a]	35	Mitchell, 1979
1979	Grant-Hidalgo County	250	25	Littauer, 1980
1988–1989	Jornada Exp. Range	26[b]	23	Del Frate, 1990
1991	Jornada Exp. Range	43	7	This report

[a] Majority of sample from Chihuahuan Desert habitat (Mitchell, pers. comm.)
[b] Authors' tabulation of age data presented in thesis

females aged 3–7 yr had ovaries with no evidence of previous estrous. Similarly, no reproduction (none of nine radio-collared females) was observed in kit foxes (*Vulpes macrotis*) during a year of drought-related prey scarcity in southern California (White and Ralls, 1993).

An extended period of below-average rainfall during 1989, 1990 and early 1991 (NOAA, 1971–1994) may have reduced prey abundance at the time of our study. Estimates of black-tailed jackrabbit (*Lepus californicus*) densities on an adjacent study site were slightly less in autumn 1990 than in autumn 1988 and 1989 (Daniel *et al.*, 1993). However, body condition of adult coyotes captured on the JER during spring 1991 appeared normal because their mean body mass-length ratio was 5% greater than in southern Texas (Windberg *et al.*, 1991). Windberg (1995) found low prey abundance did not effect body condition (body mass and fat indices) of coyotes in southern Texas. Likewise, there was no evidence that coyotes on the JER were malnourished during our study.

Although only four water sources were available on the study area during April–May 1991, that was a normal seasonal occurrence (R. P. Gibbens, pers. comm.) and hence probably had no effect on the coyote population. But an apparent physiological requirement for fluid intake by desert-dwelling canids (Golightly and Ohmart, 1984; Afik, 1989) may have dictated an arrangement of coyote territories with the water sources located along boundaries to enable use by two or more social groups on the JER.

Perhaps the best indicator of social stress in the coyote population on the JER during spring 1991 was the high percentage (40%) of transients. Two other studies found a substantially greater proportion of transient coyotes in populations during periods of low prey abundance than during comparable periods of high prey (Mills and Knowlton, 1991; White *et al.*, 1994), which suggested an interaction between prey availability and social behavior of coyotes. Also, the four radio-collared coyotes of undetermined territorial status on the JER may have been individuals that had an affiliation with territorial groups but also became transient for periods of time. Nevertheless, the social organization remained intact during spring 1991 because a network of exclusive core areas was clearly evident among the radio-collared territorial coyotes.

Windberg (1995) interpreted a negative relationship between coyote abundance and population growth in southern Texas as the effect of social factors operating in the population. He implicated the combined effect of social factors and prey availability in constraining recruitment at high (saturation) densities. In spring 1991, the coyote population on the JER was declining from relatively high abundance in the preceding year, and the 2 preceding yr of below-average rainfall probably decreased prey abundance during our study (Whit-

ford, 1976; Daniel *et al.*, 1993). Hence, the coyote population in spring 1991 may have been negatively impacted by previously high coyote abundance and declining prey abundance. The effects of those factors were expressed by low recruitment and a high proportion of transient coyotes in the population.

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